Chapter 27

Bacteria and Archaea

Lecture Outline

Overview: Masters of Adaptation

- Parts of Utah's Great Salt Lake has a salt concentration of 32%, nearly 10 times saltier than seawater.
  - Despite its harsh conditions, the lake's distinctive pink color is caused by red photosynthetic pigments produced by trillions of *Halobacteria*, a single-celled archaean.
  - This archaean is among the most salt-tolerant organisms on Earth. It pumps K^+ into its cell until the ionic concentration within the cell matches the external salt concentration.
- Many other prokaryotes are adapted to extremely harsh conditions.
  - *Deinococcus radiodurans* can survive a radiation dose of 3 million rads, while 1000 rads is fatal to a human.
  - *Picrophilus oshimae* can grow at a pH of 0.03, acidic enough to dissolve metal.
  - Some prokaryotes live in rocks 3.2 kilometers below the Earth's surface.
- Prokaryotes are adapted to a broad range of habitats, including the land and waters in which other species are found.
  - Many are also very well adapted to 'normal' habitats, lands and waters in which most other species are found.
- Today, prokaryotes still dominate the biosphere.
  - More prokaryotes inhabit a handful of fertile soil or the mouth or skin of a human than the total number of people who have ever lived.

Concept 27.1 Structural and functional adaptations contribute to prokaryotic success.

Prokaryotes are small.

- Prokaryotes were the first organisms to live on Earth.
- Most prokaryotes are unicellular, although some species aggregate transiently or permanently in colonies.
- Most prokaryotes have diameters in the range of 0.5–5 µm, compared to 10–100 µm for most eukaryotic cells.
  - The largest prokaryote discovered so far has a diameter of 750 µm, just visible to the unaided eye.
- The most common shapes among prokaryotes are spheres (cocci), rods (bacilli), and spirals.

Nearly all prokaryotes have a cell wall external to the plasma membrane.

- In nearly all prokaryotes, a cell wall maintains the shape of the cell, protects the cell, and prevents it from bursting in a hypotonic environment.
- In a hypertonic environment, most prokaryotes lose water and plasmolyze, like other walled cells.
  - This water loss inhibits the reproduction of prokaryotes, which is why salt can be used to preserve foods.
- Most bacterial cell walls contain **peptidoglycan**, a polymer of modified sugars cross-linked by short polypeptides.
  - This molecular fabric encloses the entire bacterium and anchors other molecules that extend from its surface.
  - The cell walls of archaea contain polysaccharides and proteins, but lack peptidoglycan.
- The **Gram stain** is a valuable tool for identifying bacteria based on differences in their cell walls.
  - **Gram-positive** bacteria have simple cell walls with large amounts of peptidoglycans.
  - **Gram-negative** bacteria have more complex cell walls with less peptidoglycan.
  - An outer membrane on the cell wall of gram-negative cells contains lipopolysaccharides, carbohydrates bonded to lipids.
- Among pathogenic bacteria, gram-negative species are generally more deadly than gram-positive species.
  - The lipopolysaccharides on the walls of gram-negative bacteria are often toxic, and the outer membrane protects the pathogens from the defenses of their hosts.
  - Gram-negative bacteria are commonly more resistant than gram-positive species to antibiotics because the outer membrane impedes entry of the drugs.
- Many antibiotics, including penicillin, inhibit the synthesis of cross-links in peptidoglycans, preventing the formation of a functional wall, especially in gram-positive species.
  - These drugs cripple many species of bacteria, without affecting human and other eukaryote cells that do not synthesize peptidoglycans.
- Many prokaryotes secrete another sticky protective layer of polysaccharide or protein.
  - This layer is called a **capsule** if it is dense and well defined or a *slime layer* if it is poorly organized.
- Both capsules and slime layers allow cells to adhere to their substrate or other individuals in a colony.
  - Some capsules and slime layers protect against dehydration, and some increase resistance to host defenses.
- Another way for prokaryotes to adhere to one another or to the substratum is by surface appendages called **fimbriae**, also known as *attachment pili*.
  - Fimbriae are usually more numerous and shorter than **pili**.
  - *Sex pili* are specialized for holding two prokaryote cells together long enough to transfer DNA during conjugation.

Many prokaryotes are motile.

- About half of all prokaryotes are capable of **taxis**, a directed movement away from or towards a stimulus.
  - Prokaryotes exhibiting *chemotaxis* move *towards* nutrients or oxygen (positive chemotaxis) or *away from* toxic substances (negative chemotaxis).
- Some species can move at speeds exceeding 50 μm/sec, about 50 times their body length per second.

- The beating of flagella scattered over the entire surface or concentrated at one or both ends is the most common method of movement in prokaryotes.
    - The flagella of prokaryotes differ in size, structure, and function from those of eukaryotes.
- Bacterial and archaeal flagella are similar in size and rotational mechanism, but are composed of different proteins.
    - This suggests that the flagella of bacteria, archaea, and eukaryotes arose independently. Thus they are analogous, not homologous, structures.

How did the bacterial flagellum evolve?

- The bacterial flagellum has three main parts (the motor, hook, and filament), composed of 42 different kinds of proteins.
- How could such a complex structure evolve?
    - Evidence indicates that bacterial flagella originated as simpler structures that were modified in a stepwise fashion over time.
- Biologists asked whether a less complex version of the flagellum would still benefit its owner.
- Analyses of hundreds of bacterial genomes indicate that only half of the flagellum's protein components appear to be necessary for it to function.
- Of the 21 proteins required by all species studied to date, 19 are modified versions of proteins that perform other tasks in bacteria.
    - For example, 10 proteins in the motor are homologous to 10 similar proteins in a secretory system found in bacteria. (A secretory system is a protein complex that enables a cell to secrete certain macromolecules.)
    - Two other proteins in the motor are homologous to proteins that function in ion transport.
    - The proteins that comprise the rod, hook, and filament are all related to each other, and are descended from an ancestral protein that formed a pilus-like tube.
- These findings suggest that the bacterial flagellum evolved as other proteins were added to an ancestral secretory system—an example of *exaptation*, the process in which existing structures take on new functions through descent with modification.

The cellular and genomic organization of prokaryotes is fundamentally different from that of eukaryotes.

- The cells of prokaryotes are simpler than those of eukaryotes in both internal structure and genomic organization.
- Prokaryotic cells lack the complex compartmentalization found in eukaryotic cells.
    - Instead, prokaryotes use specialized infolded regions of the plasma membrane to perform many metabolic functions, including cellular respiration and photosynthesis.
- Prokaryotes have smaller, simpler genomes than eukaryotes.
- In the majority of prokaryotes, the genome consists of a ring of DNA with few associated proteins.
- The prokaryotic chromosome is located in the **nucleoid** region.
- Prokaryotes may also have smaller rings of independently replicating DNA called **plasmids,** which consist of only a few genes.
- Although the general processes for DNA replication and translation of mRNA into proteins are fundamentally alike in eukaryotes and prokaryotes, some of the details differ.
    - For example, prokaryotic ribosomes are slightly smaller than the eukaryotic version and differ in protein and RNA content.

- These differences are great enough that selective antibiotics, including tetracycline and erythromycin, bind to prokaryotic ribosomes to block protein synthesis in prokaryotes but not in eukaryotes.

Populations of prokaryotes grow and adapt rapidly.

- Prokaryotes have the potential to reproduce quickly in a favorable environment.
  - While most prokaryotes have generation times of 1–3 hours, some species can produce a new generation in 20 minutes under optimal conditions.
  - A single cell in favorable conditions produces a large colony of offspring very quickly.
- Prokaryotes reproduce asexually via *binary fission*, synthesizing DNA almost continuously.
- Prokaryotic reproduction is limited because cells eventually exhaust their nutrient supply, accumulate metabolic wastes, face competition from other microbes, or are consumed by other organisms.
- Reproduction in prokaryotes draws attention to three key features of their biology: *They are small, they reproduce by binary fission, and they have short generation times*.
- The ability of prokaryotes to withstand harsh conditions also contributes to their success.
- Some bacteria form resistant cells called **endospores** when an essential nutrient is lacking in the environment.
  - A cell replicates its chromosome and surrounds one copy with a tough, multi-layered structure to form the endospore. Water is removed from the endospore, halting metabolism.
  - The original cell then lyses to release the endospore.
- An endospore is resistant to all sorts of trauma.
  - Most endospores can survive in boiling water. Sterilization in an autoclave kills endospores by heating them to 121°C under high pressure.
- Endospores may remain dormant but viable for centuries or longer.
  - When the environment becomes more hospitable, the endospore absorbs water and resumes growth.
- Mutation is the major source of genetic variation in prokaryotes.
- With generation times of minutes or hours, prokaryotic populations can adapt very rapidly to environmental changes as natural selection favors gene mutations that confer greater fitness.
  - As a consequence, prokaryotes are important model organisms for scientists who study evolution in the laboratory.
- Prokaryotes are highly evolved. For more than 3.5 billion years, prokaryotic populations have responded successfully to many different types of environmental challenge.

<u>Concept 27.2 Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes.</u>

- Prokaryotic populations contain considerable genetic variation.
  - For example, a ribosomal RNA gene differs more between two strains of *E. coli* than it does between a human and a platypus.
- Three factors give rise to high levels of genetic diversity in prokaryotes: rapid reproduction, mutation, and genetic recombination.

Prokaryotes' extensive genetic variation results from rapid reproduction and mutation.

- When a prokaryote reproduces by binary fission, some of the offspring differ slightly in genetic makeup due to mutation.
- The probability of a spontaneous mutation in a given *E. coli* gene is only about 1×10^{-7} per cell division. However, among the 2×10^{10} new *E. coli* cells that arise each day in a single human colon, approximately 2,000 will have a mutation in that gene.
    - When all 4,300 *E. coli* genes are considered, 9 million mutant *E. coli* cells arise per day per human host.
- The genetic diversity within a species like *E. coli* can lead to rapid evolution, as cells that are better equipped for the local environment survive and reproduce more successfully than others.

Genetic recombination is another factor that generates diversity within bacterial populations.

- Additional diversity arises from *genetic recombination*, the combining of DNA from different individuals into a single genome.
- Bacterial recombination occurs through three processes: transformation, transduction, and conjugation.
- When the individuals are members of different species, the movement of genes from one organism to another is called *horizontal gene transfer*.
- **Transformation** is the alteration of a bacterial cell's genotype – and possibly phenotype – by the uptake of foreign DNA from the surrounding environment.
    - For example, harmless *Streptococcus pneumoniae* bacteria can be transformed into pneumonia-causing cells if a live nonpathogenic cell takes up DNA that includes the allele for pathogenicity.
    - The DNA may come from dead, broken-open pathogenic cells.
    - The foreign allele replaces the native allele in the bacterial chromosome by genetic recombination, with an exchange of homologous DNA segments.
    - The resulting cell is now recombinant, with DNA derived from two different cells.
- Years after transformation was discovered in laboratory cultures, most biologists believed that the process was too rare and haphazard to play an important role in natural bacterial populations.
    - Researchers have since learned that many bacterial species have surface proteins that are specialized for the uptake of DNA.
    - These proteins recognize and transport DNA from closely related bacterial species into the cell, which can then incorporate the foreign DNA into the genome by homologous DNA exchange.
- In **transduction**, phages (viruses that infect bacteria) carry prokaryotic genes from one host cell to another, as a result of aberrations in the phage reproductive cycle.
    - A virus that carries prokaryotic DNA may not be able to replicate because it lacks some or all of its own genetic material.
    - However, the virus can attach to another prokaryotic cell (the recipient) and inject prokaryotic DNA acquired from a donor cell.
    - If some of this DNA is incorporated into the recipient cell's chromosome by DNA recombination, a recombinant cell is formed.
- **Conjugation** transfers genetic material between two bacterial cells (usually of the same species) that are temporarily joined.
    - The transfer is one-way. One cell donates DNA, and the other cell receives the genes.
- In *E. coli*, the donor cell uses a pilus to attach to the recipient.

    - The pilus retracts, pulling the two cells together, and a temporary mating bridge forms between the cells.
    - The donor cell may transfer DNA to the recipient through the mating bridge or perhaps directly through the hollow pilus.
- The ability to form a pilus and donate DNA during conjugation results from an **F factor** (F for *f*ertility) as a section of the bacterial chromosome or as a plasmid.
    - The F factor consists of about 25 genes, most required for the production of pili.
- A cell containing the **F plasmid** is designated an F^+ cell and functions as a DNA donor during conjugation.
    - A cell lacking the F factor, designated an F^- cell, functions as a DNA recipient.
    - Transfer of the entire F^+ plasmid converts an F^- cell to an F^+ cell.
- The F factor can become integrated into the bacterial chromosome.
    - A cell with the F factor built into its chromosome is called an Hfr cell (Hfr for *h*igh *f*requency of *r*ecombination).
    - Hfr cells function as donors during conjugation.
- When chromosomal DNA from an Hfr cell enters an F^- cell, homologous regions of the Hfr and F^- chromosomes may align, allowing segments of their DNA to be exchanged.
    - The result is the production of a recombinant bacterium that has genes derived from two different cells.
- In the 1950s, Japanese physicians began to notice that some bacterial strains had evolved antibiotic resistance.
    - A mutation may reduce the ability of the pathogen's cell-surface proteins to transport a particular antibiotic into the bacterial cell.
    - A mutation in a different gene may alter the intracellular target protein for an antibiotic molecule, reducing its effect.
    - Some bacteria have resistance genes coding for enzymes that specifically destroy certain antibiotics, like tetracycline or ampicillin.
- The genes conferring resistance are carried by plasmids, specifically the **R plasmid** (R for *r*esistance).
- When a bacterial population is exposed to an antibiotic, individuals with the R plasmid survive and increase in the overall population.
- Because many R plasmids also have genes that encode for pili and enable plasmid transfer, they can be transferred from one cell to another by conjugation.
- Some R plasmids carry as many as ten genes for resistance to ten different antibiotics.

Concept 27.3 A great diversity of nutritional and metabolic adaptations have evolved in prokaryotes.

- Organisms can be categorized by their nutrition, based on how they obtain energy and carbon to build the organic molecules that make up their cells.
- Nutritional diversity is greater among prokaryotes than among all eukaryotes.

- Every type of nutrition observed in eukaryotes is found in prokaryotes, along with some nutritional modes unique to prokaryotes.
  - Organisms that obtain energy from light are *phototrophs.*
  - Organisms that obtain energy from chemicals in their environment are *chemotrophs.*
  - Organisms that need only an inorganic compound such as CO_2 as a carbon source are *autotrophs.*
  - Organisms that require at least one organic nutrient—such as glucose—as a carbon source are *heterotrophs.*
- These categories of energy source and carbon source can be combined to group prokaryotes according to four major modes of nutrition.
- **Photoautotrophs** are photosynthetic organisms that harness light energy to drive the synthesis of organic compounds from CO_2 or other inorganic carbon compounds such as HCO_3^-.
  - Cyanobacteria are photoautotrophic prokaryotes.
  - Plants and algae are photoautotrophic eukaryotes.
- **Chemoautotrophs** need only an inorganic molecule like CO_2 as a carbon source but obtain energy by oxidizing inorganic substances.
  - These inorganic substances include hydrogen sulfide (H_2S), ammonia (NH_3), and ferrous ions (Fe^{2+}), among others.
  - This nutritional mode is unique to prokaryotes.
- **Photoheterotrophs** use light to generate ATP but obtain their carbon in organic form.
  - This mode of nutrition is restricted to a few marine and halophilic prokaryotes.
- **Chemoheterotrophs** must consume organic molecules for both energy and carbon.
  - This nutritional mode is found widely in prokaryotes, protists, fungi, animals, and even some parasitic plants. You are a chemoheterotroph.
- Prokaryotic metabolism also varies with respect to oxygen.
  - **Obligate aerobes** require O_2 for cellular respiration.
  - **Facultative anaerobes** use O_2 if it is present but can also grow by fermentation in an anaerobic environment.
  - **Obligate anaerobes** are poisoned by O_2 and use either fermentation or **anaerobic respiration**, in which inorganic molecules other than O_2 accept electrons from electron transport chains.
  - Such electron acceptors include nitrate ions (NO_3^-) and sulfate ions (SO_4^{2-}).
- Prokaryotes can metabolize nitrogen in a wide variety of compounds, while eukaryotes are limited in the forms of nitrogen they can use.
- **Nitrogen-fixing** prokaryotes (cyanobacteria and some archaean methanogens) convert N_2 to NH_3, converting atmospheric nitrogen to a form that they (eventually other organisms) can incorporate into organic molecules.
  - Nitrogen-fixing cyanobacteria are the most self-sufficient of all organisms, requiring only light energy, CO_2, N_2, water, and some minerals to grow.
- Prokaryotes were once thought of as single-celled individualists.
- Microbiologists now recognize that cooperation between prokaryotes allows them to use environmental resources they cannot exploit as individuals.

Cooperation may involve specialization in the cells of a prokaryotic colony.

- The cyanobacterium *Anabaena* forms filamentous colonies with specialized cells to carry out nitrogen fixation.

- Photosynthesis produces O_2, which inactivates the enzymes involved in nitrogen fixation.
- Most cells in the filament are photosynthetic, while a few specialized cells called **heterocysts** carry out only nitrogen fixation.
- A heterocyst is surrounded by a thickened cell wall that restricts the entry of oxygen produced by neighboring photosynthetic cells.
- Intercellular connections allow heterocysts to transport fixed nitrogen to neighboring cells in exchange for carbohydrates.

- In some prokaryotic species, metabolic cooperation occurs in surface-coating colonies known as **biofilms**.
  - Cells in a biofilm secrete signaling molecules to recruit nearby cells, causing the colony to grow.
  - Once the colony is sufficiently large, the cells begin producing polysaccharides and proteins that adhere the cells to the substrate and to one another.
  - Channels in the biofilms allow nutrients to reach cells in the interior and allow wastes to be expelled.
- Biofilms are common in nature, but can cause problems by contaminating industrial products and medical equipment and by contributing to tooth decay and other health problems.
  - Health and industrial damage caused by biofilms costs billions of dollars annually.
- Different species of prokaryotes may cooperate with one another.
  - Sulfate-consuming bacteria and methane-consuming archaea coexist in ball-shaped aggregates in the mud of the ocean floor.
  - The bacteria use the archaea's waste products, such as organic compounds and hydrogen.
  - In turn, the bacteria produce sulfur compounds that archaea use as an oxidizing agent when they consume methane anaerobically.
  - Each year, these archaea consume an estimated 300 billion kg of methane, a major contributor to the greenhouse effect.

Concept 27.4 Molecular systematics is illuminating prokaryotic phylogeny.

- Until the late 20th century, systematists based prokaryotic taxonomy on criteria such as shape, motility, nutritional mode, and response to Gram staining.
  - Although these criteria may be valuable in culturing and identifying pathogenic bacteria, they may not reflect evolutionary relationships.
- Applying molecular systematics to the investigation of prokaryotic phylogeny has been very fruitful.
- Microbiologists began comparing sequences of prokaryotic genes in the 1970s.
  - Carl Woese and his colleagues used small-subunit ribosomal RNA (SSU-rRNA) as a marker for evolutionary relationships.
  - They concluded that many prokaryotes once classified as bacteria are actually more closely related to eukaryotes and that they belong in a domain of their own—Archaea.
- Microbiologists have since analyzed larger amounts of genetic data, including hundreds of entire genomes.
  - They found that a few traditional taxonomic groups, such as cyanobacteria, are monophyletic.
  - Other groups, such as gram-negative bacteria, are scattered throughout several lineages.
- One important lesson that has already emerged from studies of prokaryotic phylogeny is that the genetic diversity of prokaryotes is immense.

- When researchers began to sequence the genes of prokaryotes, they could investigate only those species that can be cultured in the laboratory, a small fraction of all prokaryotes.
- Norman Pace of the University of Colorado pioneered the use of the polymerase chain reaction (PCR) to analyze the genes of prokaryotes that are collected directly from their environment, such as water or soil samples.
    - Such "genetic prospecting" is now widely used, and each year it adds new branches to the tree of life.
- Although only 7,800 prokaryotes have been assigned scientific names, a single handful of soil could contain 10,000 prokaryotic species, according to some estimates.
- Another important lesson is the significance of horizontal gene transfer in the evolution of prokaryotes.
    - Over hundreds of millions of years, prokaryotes have acquired genes from distantly related species, and they continue to do so today.
    - As a result, significant portions of the genomes of many prokaryotes are actually mosaics of genes imported from other species.
- Horizontal gene transfer can make it difficult to determine the root of the tree of life.
    - Still, it is clear that for billions of years, prokaryotes have evolved in two separate lineages: bacteria and archaea.

Researchers are identifying a great diversity of archaea in extreme environments and in the oceans.

- Archaea share certain traits with bacteria and other traits with eukaryotes.
    - Archaea also have many unique characteristics, as expected for a taxon that has followed a separate evolutionary path for so long.
- Much of the research on archaea has focused not on phylogeny but on their ecology—their ability to live where no other life can.
- The first prokaryotes to be classified in domain Archaea are species that can live in environments so extreme that few other organisms can survive there.
    - Such organisms are known as **extremophiles** or "lovers" of extreme environments.
- Extremophiles include extreme thermophiles and extreme halophiles.
- **Extreme halophiles** live in such salty places as the Great Salt Lake and the Dead Sea.
    - Some species merely tolerate elevated salinity; others require an extremely salty environment to grow.
    - For example, the proteins and cell wall of *Halobacteria* have features that function only at high salinity. These organisms cannot live below 9% salinity.
- **Extreme thermophiles** thrive in hot environments.
    - The archaean *Sulfolobus* oxidizes sulfur in 90°C sulfur springs in Yellowstone National Park.
    - At temperatures this high, the cells of most organisms die because their DNA does not stay together in a double helix, and many of their proteins denature.
    - *Sulfolobus* and other extreme thermophiles avoid this fate because their DNA and proteins have adaptations that make them stable at high temperatures.
    - One extreme thermophile that lives near deep-sea hydrothermal vents is informally known as "strain 121," since it can double its cell numbers even at 121°C.
    - *Pyrococcus furiosus* is an extreme thermophile that is used in biotechnology as the source of DNA polymerase for the polymerase chain reaction (PCR).
- Other archaea do not live in extreme environments.

- **Methanogens** obtain energy by using CO_2 to oxidize H_2, producing methane as a waste product.
  - Methanogens are among the strictest anaerobes and are poisoned by O_2.
  - Although some methanogens live in extreme environments, such as buried under kilometers of ice in Greenland, other species live in swamps and marshes where other microbes have consumed all the oxygen. "Marsh gas" is actually methane produced by archaea.
  - Other methanogens live in the anaerobic guts of animals, playing an essential role in their nutrition.
  - Methanogens are important decomposers in sewage treatment facilities.
- Many extreme halophiles and all known methanogens, plus a few extreme thermophiles, are members of a clade called Euryarchaeota.
- Most thermophilic species belong to a second clade, Crenarchaeota.
- Genetic prospecting has revealed that both Euryarchaeota and Crenarchaeota include many species of archaea that are not extremophiles.
  - These species exist in habitats ranging from farm soils to lake sediments to the surface waters of the ocean.
- New findings continue to update our understanding of archaean phylogeny.
- A new clade, Korarchaeota, was identified from archaea in a hot spring in Yellowstone National Park.
- In 2002, researchers exploring hydrothermal vents off the cost of Iceland discovered archaean cells only 0.4 µm in diameter, attached to a much larger crenarchaeote.
  - The genome of this tiny archaean is one of the smallest known of any organisms, containing only 500,000 base pairs.
  - This prokaryote belongs to a fourth archaean clade called Nanoarchaeota.
  - Three new nanoarchaeote species have since been found, one from Yellowstone's hot springs, one from hot springs in Siberia, and one from a hydrothermal vent in the Pacific.

Bacteria include the vast majority of familiar prokaryotes.

- Bacteria range from the pathogenic species that cause strep throat and tuberculosis to the beneficial species that make Swiss cheese and yogurt.
- Every major mode of metabolism and nutrition is represented among bacteria, which have a great impact on Earth and its life.

Concept 27.5 Prokaryotes play crucial roles in the biosphere.

- If humans were to disappear from the planet tomorrow, life on Earth would go on for most other species.
  - Prokaryotes are so important to the biosphere, however, that if they were to disappear, the prospects for many other species surviving would be dim.
- The atoms that make up the organic molecules in all living things were at one time part of inorganic compounds in the soil, air, and water.
- Life depends on the recycling of chemical elements between the biological and chemical components of ecosystems. Prokaryotes play an important role in this process.
- Chemoheterotrophic prokaryotes function as **decomposers**, breaking down dead organisms as well as waste products and unlocking supplies of carbon, nitrogen, and other elements essential for life.

- Prokaryotes convert inorganic compounds into forms that can be taken up by other organisms.
  - Cyanobacteria and other autotrophic prokaryotes use CO_2 to make organic compounds, which are then passed up through food chains.
  - Cyanobacteria also produce atmospheric O_2, and a number of prokaryotes fix atmospheric nitrogen (N_2) into a form that other organisms can use to make proteins and nucleic acids.
- Prokaryotes may act to *increase* or *decrease* the availability of key plant nutrients. As a result, they have complex effects on soil nutrient concentrations.
- Crenarchaeotes dominate the oceans with an estimated 10^{28} cells.
  - These abundant organisms perform nitrification and may have a large impact on the global nitrogen cycle.

Prokaryotes play a central role in many ecological interactions.

- An ecological relationship between organisms that are in direct contact is called **symbiosis**.
  - If one of the symbiotic organisms is larger than the other, it is called the **host**, and the smaller is known as the **symbiont**.
- Prokaryotes interact with other species of prokaryotes or eukaryotes with complementary metabolisms.
- In **commensalism**, one symbiotic organism benefits while the other is neither harmed nor helped by the relationship.
  - For example, more than 150 bacterial species live on the surface of your body, at densities of up to 10 million cells per cm^2. Most are commensalists.
- In **parasitism**, one symbiotic organism, the parasite, benefits at the expense of the host.
  - The **parasite** eats the cell contents, tissues, or body fluids of the host. Unlike predators, parasites do not kill the host, at least not immediately.
  - Parasites that cause disease are called **pathogens**. Many pathogens are prokaryotic.
- In **mutualism**, both symbiotic organisms benefit.
- The existence of an ecosystem may depend on prokaryotes.
  - For example, diverse ecological communities are found at deep-sea hot springs called hydrothermal vents.
  - These communities are densely populated by many different kinds of animals, including worms, clams, crabs, and fishes.
  - Since sunlight does not penetrate to the deep ocean floor, the community does not include photosynthetic organisms. Instead, the energy that supports the community is derived from the metabolic activities of chemoautotrophic bacteria.
  - These bacteria harvest the chemical energy in compounds such as hydrogen sulfide that are released from the vent.
  - An active hydrothermal vent may support hundreds of eukaryotic species, but when the vent stops releasing chemicals, the chemoautotrophic bacteria cannot survive. As a result, the entire vent community collapses.

Concept 27.6 Prokaryotes have both beneficial and harmful impacts on humans.

- Pathogenic prokaryotes represent only a small fraction of prokaryotic species.

Humans depend on mutualistic prokaryotes.

- Your intestines are home to an estimated 500 to 1,000 species of bacteria; their cells outnumber all human cells in the body by as much as ten times.
- Different bacterial species living in different portions of the intestines vary in their ability to process different foods.
- Many of these species are mutualists, digesting food that our own intestines cannot break down.
- In 2003, scientists published the first complete genome of one of these gut mutualists, *Bacteroides thetaiotaomicron.*
  - The genome includes a large array of genes involved in synthesizing carbohydrates, vitamins, and other nutrients needed by humans.
  - Signals from the bacterium activate human genes that build the network of intestinal blood vessels necessary to absorb nutrient molecules.
  - Other signals induce human cells to produce antimicrobial compounds to which *B. thetaiotaomicron* is not susceptible.
  - This action may reduce the population sizes of other, competing species, thus potentially benefiting both *B. thetaiotaomicron* and its human host.

Prokaryotes cause about half of human diseases.

- Approximately 2 million people a year die of the lung disease tuberculosis, caused by the bacillus *Mycobacterium tuberculosis*.
  - Another 2 million die from diarrhea caused by other prokaryotes.
- Lyme disease, caused by a bacterium carried by ticks that live on deer and field mice, is the most widespread pest-carried disease in the United States, infecting 15,000 to 20,000 people each year.
  - If untreated, Lyme disease can result in debilitating arthritis, heart disease, and nervous disorders.
- Pathogens cause illness by producing poisons called exotoxins and endotoxins.
- **Exotoxins** are proteins secreted by certain bacteria and other organisms.
  - Exotoxins can produce disease even if the bacteria that manufacture them are not present.
  - An exotoxin produced by *Vibrio cholerae* causes cholera, a serious disease characterized by severe diarrhea.
  - *V. cholerae* stimulates intestinal cells to release chloride ions (Cl^-) into the gut; water follows by osmosis.
  - *Clostridium botulinum*, which grows anaerobically in improperly canned foods, produces an exotoxin that causes botulism.
- **Endotoxins** are lipopolysaccharide components of the outer membrane of some gram-negative bacteria.
  - In contrast to exotoxins, endotoxins are released only when the bacteria die and their cell walls break down.
  - Endotoxin-producing bacteria include *Salmonella typhi*, which causes typhoid fever, and other *Salmonella* species, which cause food poisoning.
- Since the discovery that “germs” cause disease, improved sanitation and improved treatments have reduced mortality and extended life expectancy in developed countries.
- Antibiotics have greatly reduced the threat of pathogenic prokaryotes and have saved a great many lives.
- However, resistance to antibiotics is currently evolving in many strains of prokaryotes.

- The rapid reproduction of prokaryotes enables genes conferring resistance to multiply quickly through prokaryotic populations as a result of natural selection.
  - These genes can spread to other species by horizontal gene transfer.
- Horizontal gene transfer can also spread genes associated with virulence, turning harmless prokaryotes into potent pathogens.
- *E. coli* is ordinarily a harmless symbiont in the human intestines, but pathogenic strains causing bloody diarrhea have emerged.
  - One of the most dangerous strains is called O157:H7.
  - Today, it is a global threat, with 75,000 cases annually in the United States alone.
- In 2001, an international team of scientists sequenced the genome of O157:H7 and compared it with the genome of a harmless strain of *E. coli*.
  - Of the 5,416 genes in O157:H7, 1,387 have no counterpart in the harmless strain.
  - These 1,387 genes must have been incorporated into the genome of O157:H7 through phage-mediated horizontal gene transfer.
  - Many of the imported genes are associated with the pathogen's invasion of its host.
  - For example, some genes code for adhesive fimbriae that enable O157:H7 to attach itself to the intestinal wall and extract nutrients.
- Pathogenic prokaryotes pose a potential threat as weapons of bioterrorism.
  - In 2001, endospores of *Bacillus anthracis*, the bacterium that causes anthrax, were sent through the mail. 18 people developed inhalation anthrax and 5 died.
  - The threat of bioterrorism has stimulated intense research on pathogenic prokaryotes.

Humans have learned to exploit the diverse metabolic capabilities of prokaryotes.

- Humans have long used bacteria to make cheese and yogurt.
- Our greater understanding of prokaryotes has led to many new biotechnology applications.
  - Two examples are the use of *E. coli* in gene cloning and of *Agrobacterium tumefaciens* in producing transgenic plants such as Golden Rice.
- Bacteria can be used to make durable, biodegradable natural plastics.
  - Some bacteria synthesize a type of polyester known as PHA (polyhydroxyalkanoate), which they use to store chemical energy.
  - When these bacteria are fed sugars, the PHA they produce can be extracted, formed into pellets, and used to make plastics.
- Prokaryotes are harnessed in **bioremediation**, the use of organisms to remove pollutants from air, water, and soil.
  - Anaerobic bacteria decompose organic matter in sewage into material that can be used as landfill or fertilizer.
  - Other bioremediation applications include cleaning up oil spills and precipitating radioactive material from groundwater.
- Through genetic engineering, humans can now modify prokaryotes to produce vitamins, antibiotics, hormones, and many other products.
- Bioengineered prokaryotes can produce ethanol from agricultural waste, switchgrass, municipal waste such as paper products, and corn.
- The usefulness of prokaryotes derives from their diversity in metabolism and nutrition.